

EARLY ORDOVICIAN TRILOBITES FROM DALI, WEST YUNNAN, CHINA, AND THEIR PALAEOGEOGRAPHICAL SIGNIFICANCE

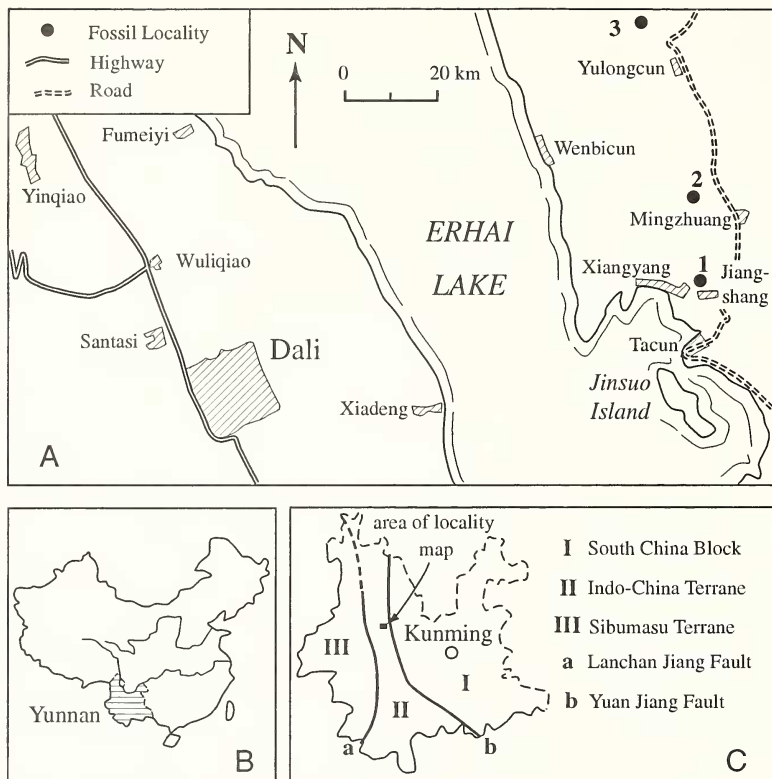
by ZHOU ZHIYI, WILLIAM T. DEAN and LUO HUILIN

ABSTRACT. Eleven late Arenig–Llanvirn trilobite taxa, including one new species, *Neseuretus elongatus*, are described from the Hsiangyang Formation east of Dali, in the eastern part of west Yunnan, China, an area that may have been part of the Indo-China Terrane. The trilobites are mostly typical representatives of Gondwana cold-water faunas, and their close biogeographical relationships with south-central Europe and the Yangtze region are discussed. Four biofacies are differentiated in relation to an environmental gradient: *Cruziana* Biofacies (intertidal); *Neseuretus* Biofacies (inner shelf); Trinucleid Biofacies (shallow outer shelf); and Cyclopygid Biofacies (deep outer shelf). The rocks of the Hsiangyang Formation are interpreted as a deepening-upwards sequence.

ORDOVICIAN rocks are exposed intermittently in the eastern part of west Yunnan, an area between the Yuan Jiang–Jinsha Jiang Fault (see Lai *et al.* 1982) and the Lancang Jiang Fault (see Fang 1991) (Text-fig. 1c). Geologically the area may have formed the northern extension of the Indo-China Terrane (Metcalf 1988, 1992), and it is bounded to the west by the Sibumasu Terrane and to the east by the South China Block. The Early Palaeozoic strata of the terrane comprise mainly metamorphic clastic rocks, with a few macrofossils reported from Cambodia, Laos, Vietnam and eastern Thailand (Workman 1977; Metcalf 1988, p. 106, fig. 5), but are otherwise little known (Scotese and McKerrow 1991, p. 276). On the Chinese side, Ordovician rocks, which are only slightly metamorphosed, contain a complete faunal succession and are best developed at Xiangyang, in the Dali area, where they have been investigated since 1945 (Sun 1945). The lower Ordovician is composed of clastic sediments; from the middle Ordovician onwards there is a progressive increase in carbonates, but only in the Caradoc do they become dominant. Trilobites occur only in the lower Ordovician but provide good evidence for considering the Indo-China Terrane as part of Peri-Gondwana during the Early Palaeozoic. Seven trilobite species recorded by Sheng (1974b) are revised on the basis of our large collection from the measured section at the stratotype, and forms new to the area are described.

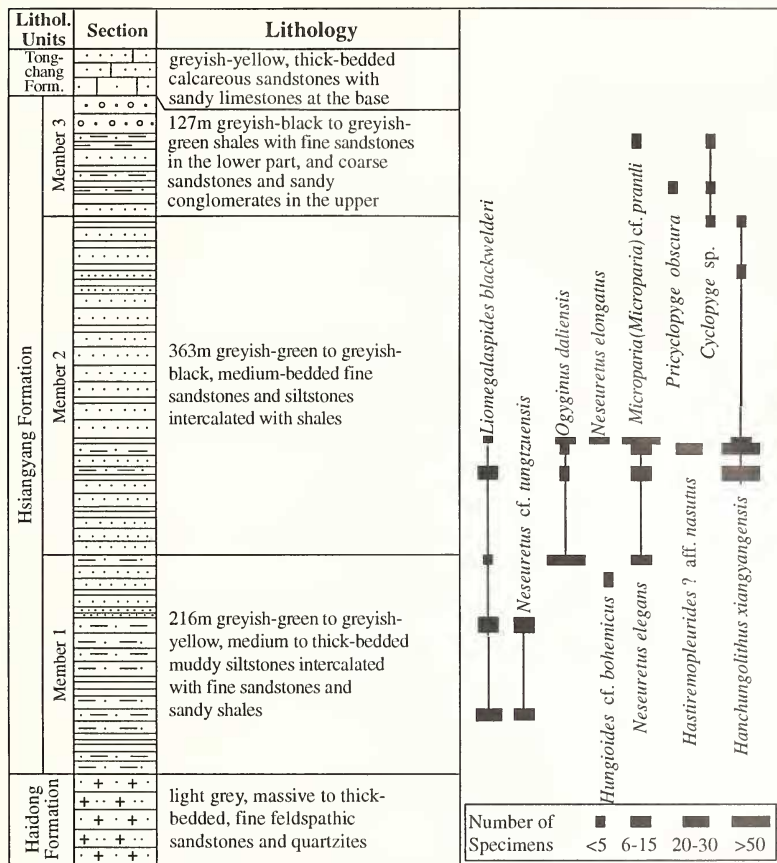
AGE AND BIOSTRATIGRAPHY

The term Hsiangyang Formation was introduced by Sun (1945) for the clastic rock sequence exposed near Xiangyang (Text-fig. 1). The lower part, comprising massive- to thickly bedded sandstones and quartzites, was later referred to a new lithostratigraphical unit, the Haidong Formation, by Sheng (1974a). The type section was measured for the first time in 1973 by the No. 1 Regional Geological Survey Team, Yunnan Bureau of Geology, who proposed its subdivision into members 1–3, in ascending order. Most of the sequence is exposed along the road from Jiangshang to Mingzhuang, but Member 3 is seen only near Yulongcun. The thicknesses of the members, and the boundaries between them, were modified slightly during field-work carried by Chen Tingen (Nanjing Institute of Geology and Palaeontology), Xiao Yinwen (No. 1 Regional Geological Survey Team, Yunnan) and the authors in the 1980s, and the revised succession is shown in Text-figure 2.



TEXT-FIG. 1. Outline maps showing position of Dali area in South-western China (B, C), and location (A) of measured sections through the Hsiangyang Formation north and east of Xiangyang.

The Hsiangyang Formation is underlain conformably by the Haidong Formation, and overlain by the Tongchang Formation; it consists mainly of siltstones, shales and sandstone, with conglomerates at the top, and the total thickness is about 700 m. Largely on the basis of trilobite evidence, the age of members 1 and 2 was considered as Llanvirn by Sheng (1974b) but as Arenig by Lai *et al.* (1982). Trilobites in our collection from members 1 and 2 are of marked Arenig-Llanvirn aspect by comparison with faunas in the Yangtze region and southern Europe (see below). The lowest fossiliferous horizon in the Hsiangyang Formation yielded *Liomegalaspides blackwelderi* and *Neseuretus cf. tungzuensis*. The former is common in the upper Arenig of southern Shaanxi (Lu 1975, p. 128, as *Isoteloides liangshanensis*) and only a single cranidium was found by



TEXT-FIG. 2. Simplified columnar section through the Hsiangyang Formation, as exposed in descending order from north to south from Yulongcun to Mingzhuang to Jiangshang, near Xiangyang, showing occurrences of identified trilobite species.

Li *et al.* (1975, p. 145, pl. 10, fig. 6, as *Megistaspis* sp.) in the Chaochiapa Formation of the same area, probably of mid Arenig age (Lai *et al.* 1982). *N. tungtzuensis* was recorded by Sheng (1958, p. 200, as *Calymene* (*Synhomalonotus*) *tungtzuensis* from the upper part of the Meitan Formation (late Arenig) in the border area between Guizhou and Sichuan. Since the distribution of shelly

faunas tends to follow shifts of facies, precise age determination based on trilobites alone can be difficult or impossible; but from their evidence it is likely that most of the rocks in Member 1 are of late Arenig age, and the base of the formation may be no older than mid Arenig.

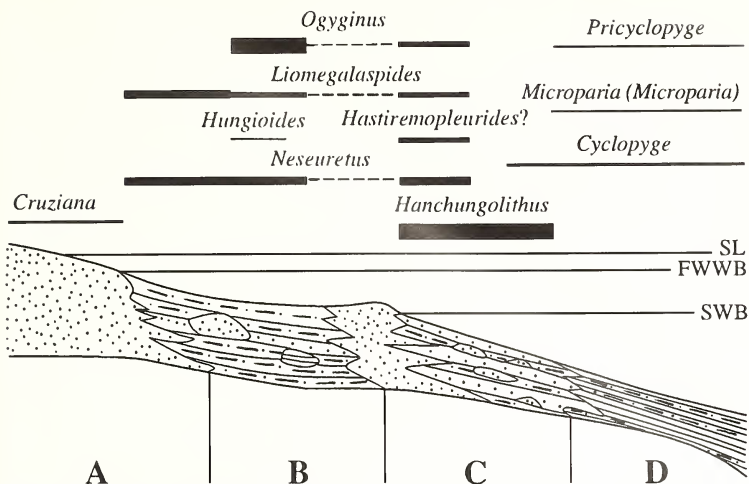
Graptolites found in association with trilobites in members 2 and 3 have been identified by Ni Yunan (Nanjing Institute of Geology and Palaeontology). They include, *inter al.*: *Amplexograptus confertus* (Lapworth), *Didymograptus artus* Elles and Wood and *D. nanus* Lapworth from Member 2; and *Didymograptus jiangxiensis* Ni and *D. murchisoni* Beck from the lower part of Member 3. The material, which has not yet been described, indicates that Member 2 may be correlated approximately with the *D. artus* Biozone (early Llanvirn) and Member 3 with the *D. murchisoni* Biozone (late Llanvirn). Trilobites are rare in Member 3 and all belong to the Cyclopygidae, including *Cyclopyge* sp., *Microparia* (*Microparia*) cf. *prantli* and *Pricyclopyge obscura*. *M. (M.) prantli* and *P. obscura* have been recorded only from the Llanvirn of Bohemia (Marek 1961). Specimens of *Cyclopyge* sp., although poorly preserved, are closely related to *C. kossleri* from the Llanvirn of Bohemia (Marek 1961) and South Wales (Fortey and Owens 1987). No macrofossils were found in the highest part of the formation, and the conglomerates may have formed during regression in the latest Llanvirn.

BIOFACIES AND PALAEOENVIRONMENTS

The Haidong Formation, the lowest part of the Ordovician succession in the Dali area, contains no trilobite body fossils but the trace fossil *Cruziana* and the inarticulate brachiopod *Lingulepis* have been found at several levels, suggesting a littoral environment, above wave base (Crimes 1970). Most of the thickly to massively bedded arenite deposits are fine-grained and well-sorted, and low-angle cross-beds a few metres thick appear at several levels; all indicate intertidal conditions (Text-fig. 3A).

Most fossils from Member 1 of the Hsiangyang Formation were found in siltstones; only bivalves are known from the basal strata, but in higher beds they are accompanied by the trilobites *Neseuretus* cf. *tungtzuensis* and *Liomegalaspides*. Trilobites become progressively more diverse higher in the succession, in the upper part of which *Hungioides* and *Ogyginus* make their appearance and *N. cf. tungtzuensis* is replaced by *Neseuretus elegans*. The trilobite association is characterized by *Neseuretus* and asaphids, indicating the *Neseuretus* Biofacies (cf. *Neseuretus* Community of Fortey and Owens 1978). The fauna represents a shallow-water, inner shelf environment (Fortey and Owens 1978, p. 238; see Text-fig. 3B). Storm-induced bioclastic beds appear at several levels, formed by abundant shelly debris that includes bivalves and a few trilobites and brachiopods. Intercalations of sandy shale resting on siltstone are largely lenticular and show wave-ripple laminations, while hummocky cross-stratification is seen locally within a few siltstone beds. The sedimentary evidence suggests, according to Prothero and Schwab (1996), that Member 1 was formed in the zone below fair weather wave base and above storm wave base. Trilobite diversity in the *Neseuretus* assemblage is low and no planktic taxa, such as graptolites, are known from Member 1. Most of the siltstone beds are horizontally stratified and the less weathered rocks are black; some trilobites are preserved as complete exoskeletons, and disarticulated specimens remain unbroken. It is likely that most rocks of Member 1 were deposited under quiet conditions between intervals of storm re-working. The inner shelf may have been bordered by small, discontinuous rises that made faunal exchange incomplete, and the alternations of fossiliferous and barren beds may indicate rapid fluctuations in oxygen content. *Cruziana* and *Lingulepis* continue upwards from the Haidong Formation and have been found, although without other associated macrofossils, in a few intercalated sandstone beds in the lower part of Member 1; these occurrences suggest occasional relative falls in sea level during the interval represented by Member 1.

Member 2 begins with about 80 m of medium- to thickly bedded fine sandstones, in the middle of which are a few beds of sandy shale. No fossils have been found in these beds, the sand grains are mature and well sorted, and several beds show hummocky cross-stratification. The sandstones are capped by grey to black shales and siltstones, finely and horizontally laminated, and rich in



TEXT-FIG. 3. Model showing palaeogeographical distribution of trilobites of the Hsiangyang Formation in relation to biofacies. A, *Cruziana* Biofacies (intertidal shore); B, *Neseuretus* Biofacies (inner shelf); C, Trinucleid Biofacies (shallow outer-shelf); D, Cyclopygid Biofacies (deep outer-shelf). SL = sea-level; FWWB = fair-weather wave base; SWB = storm wave base.

trilobites and graptolites. About 20 per cent. of the trilobites collected are preserved as articulated exoskeletons, a few of which are undisturbed, *in situ* moults (Pl. 3, fig. 11). Others are disarticulated, but the various parts of a single individual may sometimes be found associated on the same bedding plane. All these features suggest quiet conditions of deposition well below storm wave base. The trilobite fauna consists of *Hanchungolithus*, *Hastiremopleurides?*, *Liomegalaspides*, *Neseuretus* and *Ogyginus*. Compared with the fauna of Member 1, *Hanchungolithus* is both a characteristic new addition and a dominant element, accounting for 50 per cent. of the total specimens from this horizon, for which the term Trinucleid Biofacies is employed. Zhou *et al.* (1990, 1992) suggested that the Trinucleid Biofacies represents a shelf-slope environment (depth < 100 m) with a muddy or clastic substrate.

A similar sequence, passing from fine sandstone to shale, appears again in the middle and upper parts of Member 2, following fluctuations in sea-level, but most of the trilobite genera are absent, except for *Hanchungolithus*, which is associated with *Cyclopyge* in an horizon at the top. Cyclopygids have been considered as mesopelagic trilobites, distributed in a depth zone of some 200–700 m (Fortey 1985). However, as pointed out by Zhou *et al.* (1994), on the basis of their palaeogeographical distribution there may have been a depth-induced differentiation between cyclopygids of superficially similar morphology. Of these, *Cyclopyge* is one of a few genera that lived at a shallower water level and may have penetrated shallower shelf areas during periods of transgression. We believe that most of the shales and siltstones in Member 2 were formed on the shallow outer shelf, and that the sandstones may represent small, low sand bars distributed along the margin of the inner shelf (Text-fig. 3c).

Member 3 is made up of probable turbiditic deposits. About 40 m of argillaceous to arenaceous beds in the lower part show planar laminations, whilst shaly or muddy siltstones, sandy mudstones

and mudstones were rhythmically deposited. Only planktic faunas have been found, including graptolites and cyclopygid trilobites (*Cyclopyge*, *M. (Microparia)*, *Pricyclopyge*), but they are not abundant. The trilobite association indicates the Cyclopygid Biofacies which, for Fortey and Owens (1987), generally represents marine conditions about 300 m deep. However, Fortey and Owens (1987) stated that 'in more turbid epicontinental seas [light penetrated] to less than half this depth', and Zhou *et al.* (1990, 1992) pointed out that the exact water depth often depends on the clarity of the water body. The turbidity current induced deposits of Member 3 may indicate generally turbid marine conditions in this area during the late Llanvirn, and from the regional facies context we infer a depth of less than 200 m. About 75 m of arenites overlying the shales are mainly poorly sorted, thickly bedded, fine conglomerates and coarse sandstones that pass laterally into fine sandstones. This set of coarse clastics is considered to represent debris flows from adjacent shallow areas during the latest Llanvirn regression (see Fortey 1984). Debris flows appear also at the top of Member 2 and in the lower part of Member 3, but are thinner. It is likely that Member 3 was deposited on the lower shelf slope or the deep outer shelf (Text-fig. 3d).

In general, the succession from the Haidong Formation to the Hsiangyang Formation indicates a deepening-upwards sequence, although small-scale fluctuations in sea-level were frequent. Four facies types, separated by transitional boundaries, are differentiated in relation to the shallow to deeper water environmental gradient.

FAUNAL AFFINITIES AND PALAEOGEOGRAPHICAL IMPLICATIONS

Of the nine genera recorded from the late Arenig to Llanvirn Hsiangyang Formation, four (*Neseuretus*, *Ogyginus*, *Hanchungolithus* and *Hungioides*) are well known as typical benthic index fossils of Ordovician Gondwanaland, and their geographical distribution is summarized below. Unless otherwise stated, the relevant tectonic regions listed here are those of Scotese and McKerrow (1991, fig. 1).

1. *Neseuretus*. Arenig: Wales, England, Germany, south-western France, eastern Newfoundland, Morocco, Algeria, southern Turkey, and the Yangtze region of the South China Block. Llanvirn: Argentina, Bolivia, Peru, England, Spain, Morocco, Algeria, Saudi Arabia, Burma and the western part of west Yunnan (the two last-named areas belong to the Sibumasu Terrane). Llanvirn to Llandeilo: south-western England (Cornwall), north-western France, Spain, Portugal, Algeria, Tunisia and Morocco (see Fortey and Morris 1982; Dean 1985; Zhou and Dean 1989; Rabano 1990).
2. *Ogyginus*. Arenig: Wales, south-western France and eastern Newfoundland; Llanvirn: Wales, England, ?Spain, ?Portugal, and possibly Argentina, Bolivia and Peru (as *Hoekaspis*, see below); Arenig-?Llanvirn: north-western France; Llanvirn-Llandeilo: England and Wales (see Romano *et al.* 1986; Fortey and Owens 1987; Rabano 1990).
3. *Hanchungolithus*. Middle Arenig: south-western France, south-eastern Ireland and ?North Wales; upper Arenig: the Yangtze region (see Hughes *et al.* 1975; Zhou and Hughes 1989).
4. *Hungioides*. Tremadoc: the Yangtze region; Arenig: central Australia, the Yangtze region, Inner Mongolia (western marginal area of the North China Block) and ?south-western France; Llanvirn: Bohemia, Germany, Spain, Portugal and Argentina (see Rabano 1983; Zhou and Dean 1989).

Two further benthic trilobite genera, *Liomegalaspides* and *Hastiremopleurides*?, are more endemic, recorded only in parts of eastern Gondwanaland. The former is known mainly from the upper Arenig to lower Llanvirn of the Yangtze region, Central and Southwest China, and the Tarim region, Northwest China. *Hastiremopleurides*? is considered to represent a group of species with well-developed triangular anterior border that was confined to the Yangtze region from the Arenig to Caradoc, but probably migrated to south-eastern Turkey in the early Ashgill (see below).

Mesopelagic trilobites are represented only by *Cyclopyge*, *M. (Microparia)* and *Pricyclopyge*, members of a family confined mainly to peripheral Gondwana, especially in the early Ordovician (Fortey and Owens 1987, p. 108).

Three of the 11 species present are conspecific with, or closely related to, forms from the Yangtze region: *Neseuretus* cf. *tungtzuensis*, *Liomegalaspides blackwelderi* and *Hastirenopleurides?* aff. *nasutus*. A further three (*Neseuretus elegans*, *Ogyginus daliensis* and *Hungioides* cf. *bohemicus*) exhibit close relationships to south and central European species (*Neseuretus arenosus*, *Ogyginus armoricanus* and *H. bohemicus*). Cyclopygid species are usually widespread, and the three species in the Dali area closely resemble coeval Bohemian forms. If the eastern part of west Yunnan formed a northward extension of the Indo-China Terrane, as deduced by Metcalfe (1988, 1992), the trilobite evidence may indicate a biogeographical connection between the South China Block, south-central Europe, and the Indo-China Terrane. Interestingly, the appearance of the above benthic trilobite genera in the Indo-China Terrane is not exactly contemporaneous with their corresponding appearance in south-central Europe or the Yangtze region. A typical example is *Hanchungolithus*, which occurs in the middle Arenig of south-western France and south-eastern Ireland, in the upper Arenig of the Yangtze region, and in the lower Llanvirn of the Dali area. This indicates that free migration or dispersal of trilobites was possible along the epicontinental sea on the east side of the 'Paleotethys Ocean' of Scotese and McKerrow (1991; discussion in Dean 1967b, p. 23; El-Khayal and Romano 1985, p. 404).

Neseuretus was interpreted by Fortey and Morris (1982) as representative of shallow, cold-water Gondwana faunas found only at high latitudes. An exception to this is the northward extension of the genus into the Yangtze Carbonate Platform, the explanation for which may involve either the northward movement of a cold ocean current into lower latitudes, or even differences in water depth. We agree with Fortey and Owens (1987) that the *Neseuretus* Biofacies represents an inner shelf environment. However, the palaeogeographical distribution in the Dali area (Text-fig. 3) indicates that *Neseuretus* itself may have had a wider tolerance range, from inner shelf to shallow outer shelf. In south-western France (Dean 1966) *Neseuretus* was described from graptolite-bearing mid Arenig mudstones, in association with *Hanchungolithus*, and more recently it was found in the upper Arenig (*U. austrodeniatus* Zone) of western Hubei (Xiang and Zhou 1987), with *Nileus*, a warm-water trilobite usually considered to occupy a farther off-shelf habitat than *Neseuretus*.

The Armorican types of clastic facies and the cold-water trilobites assemblages in the Dali area suggest that, at least in the early Ordovician, the Indo-China Terrane may have been located at a higher latitude than shown by Metcalfe (1992, fig. 4) and by Scotese and McKerrow (1991, fig. 3). It is highly likely that the Indo-China Terrane was situated closer to the south-central Europe Block than to the South China Block. West of the Indo-China Terrane, Ordovician rocks are documented in the Baoshan area, western west Yunnan (Lai *et al.* 1982), the Shan States (Chhibber 1934) and the Thailand-Malaysia border area (Hamada *et al.* 1975). Contiguity of lithological and faunal successions in the first two areas was noted by Sun and Szetu as early as 1947, and the lower Ordovician there comprises mainly clastics with only a few limestones in the upper part; in marked contrast, the succession in the last-named area is composed essentially of carbonates. These differences were interpreted by Metcalfe (1992) as due to facies changes on a single stable shelf which belonged to the Sibumasu (or Shan-Thai) Terrane. No reliable evidence of Arenig trilobites is known from this terrane, but the Llanvirn trilobite *Basilicus* (*Basilicus*) *satunensis* (Kobayashi and Hamada, 1964, p. 208, pl. 9, figs 1-12), from Satun, near the Malaysian frontier with Thailand, exhibits close affinities with *B. (B.) boehmi* (Lorenz) from the coeval Machiakou Formation in North China (see Zhou and Fortey 1986, p. 180; Zhou and Dean 1989, p. 132). Llanvirn trilobites from the Baoshan area (Reed 1917; Sheng 1974b) and North Shan States (Reed 1906, 1915) include, *inter al.*, *Neseuretus*, *Prionocheilus*, *Basilicus* (*Basilicella*) [as *Pseudobasilicus baoshanensis*; see Sheng 1974b, p. 101, pl. 3, fig. 3], *Encrinurella* and *Pliomerina*. Species of *B. (Basilicella)* and *Pliomerina* are closely similar to those from the Machiakou Formation of North China and the Tsuibon Formation of South Korea (Zhou and Fortey 1986, pp. 182, 202), whilst *Encrinurella* is known elsewhere only from the lower Ordovician in Australia (Legg 1976). A south-western Gonwanaland connection is also indicated by *Neseuretus* and *Prionocheilus*. On the whole, the Llanvirn trilobites of the Sibumasu Terrane differ markedly from those of the Indo-China Terrane, suggesting geographical separation of the two areas. Based on the similarity of early Ordovician nautiloids from the

Thailand-Malaysia border area, North China and Australia, Burrett and Stait (1987, fig. 7) and Burrett *et al.* (1990, fig. 4) considered the Sibumasu Terrane to be located in the tropics, in the proximity of the North China and Australia blocks. However, the trilobite evidence favours the reconstructions by Scotese and McKerrow (1991, fig. 3) and by Metcalfe (1992, fig. 4), in which the Sibumasu Terrane was rotated through 180° so that Thailand Peninsula-West Malaysia was on the palaeoequator, close to the North China Block, while the Shan States-western west Yunnan area may have been sited in a low latitudinal zone not far from the South China Block.

SYSTEMATIC PALAEOLOGY

The terminology adopted here is that of Harrington *et al.* (*in* Moore 1959, pp. 117–126), with modifications by Whittington and Kelly (*in* Kaesler 1997). Described and cited specimens are housed in the following institutions, with prefixes for registration numbers: BGM, Geological Museum of Beijing, Ministry of Geology and Mineral Resources; CIGM, Chendu Institute of Geology and Mineral Resources, Academy of Geological Sciences of China; NI, Nanjing Institute of Geology and Palaeontology, Academia Sinica; SBNM, National Museum of Natural History, Prague; USNM, National Museum of Natural History, Washington, D.C.

Family REMOPLEURIDIDAE Hawle and Corda, 1847
Subfamily REMOPLEURIDINAE Hawle and Corda, 1847

Genus HASTIREMOPLEURIDES Yin, 1980

Type species. Remopleurides (Hastiremopleurides) bijieensis Yin, 1980.

Hastiremopleurides? aff. *nasutus* (Lu, 1957)

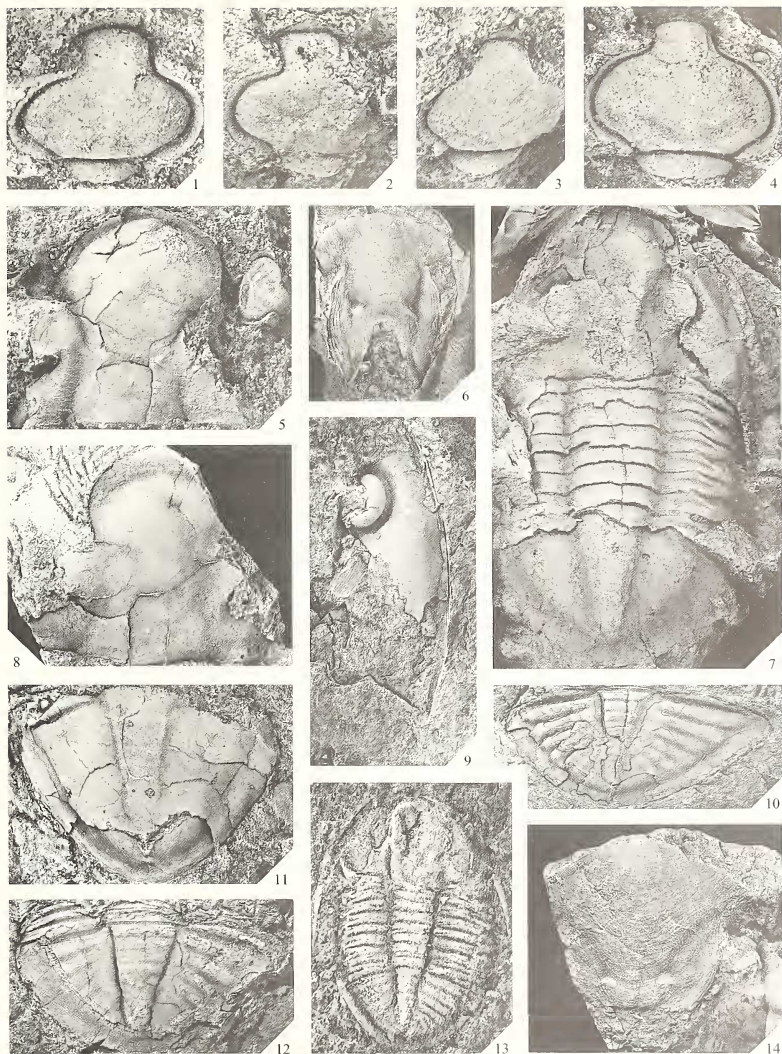
Plate 1, figures 1–4

1974b *Remopleurides cf. dalecarlicus* Holm; Sheng, p. 99, pl. 1, fig. 4a–f.

Description. Cranium pitcher-shaped in outline, weakly convex, its length 85–100 per cent. the breadth; downturned anterior tongue expands forwards slightly and has basal width about 32–35 per cent. the maximum cranial breadth, across the mid-point of the palpebral lobe. Glabella has deeply incised, transverse S0 and three pairs of faint, subparallel, equispaced lateral furrows. S1 and S2 are gently sigmoidal, S3 is straighter, and all become successively shorter and weaker from S1 to S3; the furrows do not reach the axial furrows, and extend slightly backwards adaxially; the distal end of S1 almost coinciding with the maximum breadth of the cranium. Occipital ring occupies 56–63 per cent. the cranial width, and about 14 per cent. the length (sag.) of the glabella in specimens preserved in relief; it declines and becomes slightly narrower (exsag.) abaxially, and a median node is sited close to S0. Palpebral lobe strongly convex in plan, widens posteriorly and extends from S0 to base of anterior tongue; palpebral or axial furrow deep. Anterior area of

EXPLANATION OF PLATE 1

- Figs 1–4. *Hastiremopleurides?* aff. *nasutus* (Lu, 1957); Loc. 1, Member 2. 1, NI 127486; cranium; × 10. 2, NI 127487; cranium; × 7. 3, NI 127488; cranium; × 8. 4, NI 127489; cranium; × 6.
Figs 5–9, 11. *Liomegalaspides blackwelderi* (Weller, 1907). 5, NI 127490; cranium; Loc. 1, Member 2; × 3. 6, NI 127491; hypostoma; Loc. 2, Member 1; × 1.5. 7, NI 127492; exoskeleton, latex cast from external mould; Loc. 2, Member 1; × 3. 8, NI 127493; cranium; Loc. 2, Member 1; × 3. 9, NI 127494; librigena; Loc. 1, Member 1; × 2. 11, NI 127495; pygidium; Loc. 1, Member 2; × 1.5.
Figs 10, 12–14. *Ogyginus daliensis* (Sheng, 1974b); Loc. 1. 10, NI 127496; pygidium; Member 1; × 1.2; 12, NI 127497; pygidium; Member 2; × 1. 13, NI 127498; exoskeleton, meraspid degree 7; Member 2; × 6. 14, NI 127499; hypostoma; Member 2; × 2.



fixigena narrow (tr.), triangular, depressed. Anterior border upturned, triangular in plan, bluntly pointed frontally. Border furrow deep and merges with preglabellar furrow in front of anterior glabellar tongue.

The librigena as illustrated by Sheng (1974b, pl. 1, fig. 4b-c) is very narrow outside the eye, flat anteriorly, and convex behind the base of the librigenal spine. Eye semicircular, its width 60 per cent. that of librigena, and its posterior half more strongly curved than the anterior half; the visual surface declines gently at first but becomes almost vertical peripherally. Eye socle narrow, upturned, defined above and below by deep furrows. Librigenal spine slightly curved, its length at least twice that of librigena, and its broad base in-line with midpoint of eye; lateral margin joins that of anterior half of librigena in a broad curve; intergenal angle (= genal notch of authors such as Nikolaisen 1983) about 45° and deep.

Remarks. Sheng (1974b) compared this form with *Remopleurides dalecarlicus* Holm, in Warburg (1925, p. 88, pl. 1, figs 7-8; pl. 11, fig. 34), from the Upper Leptaena [= Boda] Limestone (Ashgill) of Dalarna, Sweden. Material in our collection shows the cranium to have a broad (sag.) anterior border, a single character sufficient to exclude the species from *Remopleurides*. In our opinion the species is closely related to *Remopleurides nasutus* Lu, 1957 (p. 277, pl. 153, figs 14-15), a taxon redescribed by Lu (1975, p. 299, pl. 3, figs 15-22; pl. 4, figs 1-13) from the upper Arenig of southern Shaanxi and western Hubei, China, and later recorded from northern Guizhou (Yin, in Yin and Lee 1978, p. 519, pl. 172, fig. 2) and southern Anhui (Zhang Quanzhong, in Qiu *et al.* 1983, p. 196, pl. 65, fig. 6; as *Remopleurides latlingulatus*, placed here in synonymy with *nasutus*). The glabella, excluding occipital ring, is 75-80 per cent. as long as wide, and anterior tongue has width 26-43 per cent. (depending on preservation) that of glabella in our specimens; the corresponding figures in *R. nasutus* are 74-90 per cent. and 37-53 per cent., underlining the similarity of the cranium in both forms. Other characters, such as the lateral glabellar furrows, palpebral lobe, occipital ring and anterior border, are almost identical in the late Arenig and Llanvirn specimens; but *R. nasutus* differs in the more posterior position of the librigenal spine base, which extends from the lateral margin of the librigena at a point about one-third its length from the rear.

The species also resembles *Remopleurides shihtzupuensis* Lu, 1957 (p. 278, pl. 153, fig. 16; 1975, p. 301, pl. 4, figs 14-15) from the Shihztzupu Formation (Llandeilo) of northern Guizhou; Lu considered the latter to have a narrower anterior glabellar tongue than *R. nasutus*, but in the holotype (Lu 1957, pl. 153, fig. 16) its basal width is 34 per cent. that of the glabella, similar to the present material. However, the genal spine in *shihtzupuensis* is based on the anterior part of the librigena (Zhou *et al.* 1984, p. 15, fig. 3a-b), which is more advanced than in the present form.

We believe that these three closely allied species may represent a new genus, the cranium of which has a characteristic triangular anterior border. The more transverse, faint to shallow lateral glabellar furrows recall *Remopleurides*, and the narrow librigena with deep intergenal angle is similar in certain species of that genus; but, in addition to the very different preglabellar area, the pygidium in *R. nasutus* has a much longer outer (= first) pair of pleural spines, and a shorter inner pair. In the shape and size of the anterior border and the anterior cranial tongue, it resembles *Arator* Nikolaisen, 1991, type species *Robergia marianna* Koroleva, 1965, from the lower middle Ordovician of northern Kazakhstan; but the latter differs mainly in the deeply incised, less anteriorly divergent lateral glabellar furrows, and in having a rectangular pygidium with three pairs of pleural spines.

The above three Chinese species are of different ages but have a similar cranium, and local gradual morphological changes can be recognized in the librigena. They involve mainly the librigenal spine, which becomes successively more anterior in position: its base is opposite the rear part of the eye in *nasutus*, the earliest (Arenig) form; the middle part in the Llanvirn aff. *nasutus*; and the front part in the Llandeilo *shihtzupuensis*. The three species may possibly form a peramorphocline in this character.

Nikolaisen (1983, p. 277) suggested that some early species, such as *R. nasutus* and *R. shihtzupuensis*, may belong to an ancestral genus, which he called '*Robergiella* s.l.', and may have evolved into his younger genus *Sculptaspis*. Both species are comparable to members of *Robergiella* Whittington, 1959, in the form of the lateral glabellar furrows and the pygidium, but even in early species such as *R. brevilingua* Fortey, 1980 (p. 44, pl. 5, figs 1-8, 10-11; pl. 25, figs 7, 11, 13) and

R. hundehukensis Fortey, 1980 (p. 46, pl. 5, figs 9, 12–14, 16), both from the Arenig of Spitsbergen, the anterior cranial tongue has only a very narrow (sag.) frontal rim, and the librigena has a broader genal field between the eye socle and border. It is likely that the group of Chinese species is independent of both *Robergiella* and *Sculptaspis*. The latter is closely similar to *Sculptella* Nikolaisen, 1983, although, as noted by Nikolaisen (1983, pp. 267, 277), it has a thicker exoskeleton and the outer margin of the librigenal spine is at a distinct angle to the lateral border of the librigena. Species of both Nikolaisen's genera may be compared to the group of Chinese species but differ in: the narrower anterior glabellar tongue, the longer postaxial field of the pygidium, and the form of the librigena, in which the librigenal spine is located more posteriorly and the intergenal angle is very shallow.

Nikolaisen (1983, p. 266) postulated an evolutionary lineage from *Remopleuridiella* Ross, 1951, by way of *Sculptella* and *Remopleurella* Dean, 1963 to *Amphitryon* Hawle and Corda, 1847. Morphological changes affecting the librigena during phylogeny involve a rearward shift of the base of the librigenal spine, and progressive shallowing of the librigenal notch, culminating in its eventual disappearance; these suggest that local heterochronic variation may have occurred by pedomorphosis. If the lineage postulated by Nikolaisen proves to be correct, then, at least on the basis of the evolution of the librigena, the group of Chinese species may form a different remopleuridid lineage.

Robergia striata Endo, 1932 (p. 109, pl. 38, fig. 3), from an unstated horizon at Huangbayi, southern Shaanxi, was reassigned to *Remopleurides* by Reed (1935), Kobayashi (1951), Whittington (1959), Lu *et al.* (1965), Li *et al.* (1975) and Chang and Jell (1983). Li *et al.* (1975, p. 151) reported the species from the Pagoda Formation (Caradoc) at its type locality, and similar cranidia were later described from the same formation at Liangshan, Hanzhong, southern Shaanxi (Ji 1986, p. 12, pl. 1, figs 13–14). The holotype, refigured by Chang and Jell (1983, fig. 6E–F), closely resembles cranidia in our collection, but its anterior glabellar tongue is wider, 46 per cent, the glabellar width. Nikolaisen (1991, p. 54) was inclined to refer *R. striata* to *Sculptaspis*, but the wider cranial tongue and the shape of the anterior border suggest, rather, the *nasutus*-group.

Outside China, *Amphitryon?* sp. from the lower Ashgill of south-eastern Turkey (Dean and Zhou 1988, p. 643, pl. 61, figs 8–10) is closely related to the group of Chinese species; the anterior cranial tongue is narrower (tr.) in the Turkish species, but the length of the triangular anterior border is similar to that of *nasutus*.

Zhou *et al.* (1984, p. 15) assigned *shihtzupuensis* to *Hastiremopleurides*. The type species, *H. bijiensis* Yin (1980, p. 23, pl. 1, fig. 6) from the Chientsaokou Formation (lower Ashgill) of Bijie, northern Guizhou, has the anterior glabellar tongue more expanded frontally, with a much longer (sag.) anterior border, but is otherwise basically similar to all the species in the *nasutus*-group. Immature specimens of *nasutus* show that the length (sag.) of the anterior border increased during ontogeny (Lu 1975, p. 300). This may suggest a peramorphic increase in border length, and *bijiensis* might represent the latest stage of one branch in the *nasutus* evolutionary series. Unfortunately, except for *nasutus*, material is limited and species in this series are imperfectly known, so that for the time being we refer both *nasutus* and the present material with reservation to *Hastiremopleurides*.

Family ASAPHIDAE Burmeister, 1843

Subfamily ISOTELINAE Angelin, 1854

Genus LIOMEGALASPIDES Lu, 1975

Type species. Isotelus usuii Yabe, in Yabe and Hayasaka, 1920.

Liomegalaspides blackwelderi (Weller, 1907)

Plate 1, figures 5–9, 11

- 1907 *Asaphus blackwelderi* Weller, p. 560.
 1907 *Asaphus asiaticus* Weller, p. 561.
 1913 *Asaphus blackwelderi* Weller; Weller, p. 286, pl. 26, figs 21–22.
 1913 *Asaphus asiaticus* Weller; Weller, p. 287, pl. 26, fig. 5.
 1957 *Isotelooides liangshanensis* Lu, p. 279, pl. 152, figs 1–2.
 1974b *Pseudoasaphus daliensis* Sheng, p. 101, pl. 4, fig. 1a–b, f (non c–e).
 1975 *Isotelooides liangshanensis* Lu, p. 322, pl. 9, figs 6–10; pl. 10, figs 1–11.
 1975 *Megistaspis* sp. Li *et al.*, p. 145, pl. 10, fig. 6.
 1975 *Isotelooides liangshanensis* Lu; Li *et al.*, p. 147, pl. 13, fig. 5.
 1982 *Isotelooides liangshanensis* Lu; Zhou *et al.*, p. 263, pl. 65, fig. 16.
 1983 *Megalaspides blackwelderi* Weller; Chang and Jell, p. 198, fig. 3B, H–1 [non figs 3A, C–G, 4J, 5E = *Megalaspides taningensis* (Weller)].

Holotype. Cranium (USNM 60876) figured Weller, 1913, pl. 26, fig. 21 (see also Chang and Jell 1983, fig. 3B), from an Arenig limestone, 2.4 km upstream from Sukiapa on the Taning River, northern Sichuan.

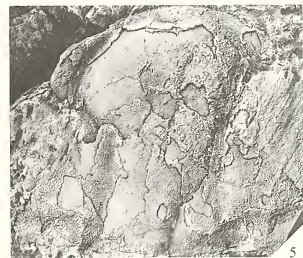
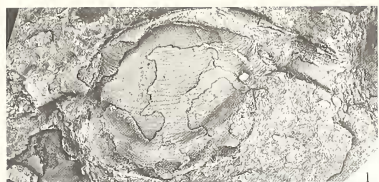
Figured specimens. One exoskeleton (NI 127492), one cranium (NI 127493) and one hypostoma (NI 127491) from Member 1, Loc. 2; one cranium (NI 127490), one librigena (NI 127494) and one pygidium (NI 127495) from Member 2, Loc. 1.

Remarks. One cranium, one small, compressed pygidium and three librigenae from Member 2, Loc. 1, were described by Sheng (1974b) as a new species, *Pseudoasaphus daliensis*. The cranium (BGM OT68-48, 49; Sheng 1974b, pl. 4, fig. 1a–b), selected herein as lectotype, has a small palpebral lobe, its anterior margin level with the centre of the cranium; the glabella lacks a posterolateral glabellar furrow and a distinct occipital ring. The pygidium (Sheng 1974b, pl. 4, fig. 1f) shows a narrow doublure. All these characters suggest that assignment of the species to *Pseudoasaphus* Schmidt, 1904 is incorrect. In the light of the present collection, the librigenae figured as *P. daliensis* by Sheng (1974b, pl. 4, fig. 1c–e) may belong to *Nesewretus elongatus* sp. nov. (see below).

The new material indicates that *daliensis* is synonymous with *Isotelooides liangshanensis* Lu (1975), from the *Ningjianolithus welleri* Zone (uppermost Arenig) in the Siliangssu Formation of southern Shaanxi. Lu's species is characterized by the following features: (1) the cephalon is sub-triangular in outline; (2) the glabella is broadly rounded anteriorly, constricted between the palpebral lobes and poorly defined; (3) the anterior sections of the facial suture are divergent instead of subparallel; (4) the acute posterior area of the fixigena shows no border furrow in testaceous material; (5) the pygidium is triangular, with smooth surface and a narrow but concave doublure. Judging from better preserved material (Lu 1975, pl. 9, figs 7, 9–10; pl. 10, figs 2, 8; Li *et al.* 1975, pl. 13, fig. 5), the pygidium has no defined border, and the supposed 'border furrow' is seen only in compressed specimens; the width (sag.) of the anterior border of the cranium appears to vary from wide (Lu 1975, pl. 9, fig. 8) to narrow (Lu 1975, pl. 10, fig. 2), and in some examples the border merges with

EXPLANATION OF PLATE 2

- Figs 1–6, 9. *Ogyginus daliensis* (Sheng, 1974b); Member 1. 1, NI 127500; hypostoma with attached cephalic doublure; Loc. 1; $\times 3$. 2, NI 127501; cranium; Loc. 1; $\times 1.2$. 3, NI 127502; exoskeleton without librigenae; Loc. 2; $\times 2$. 4, NI 127503; exoskeleton; Loc. 1; $\times 0.6$. 5, NI 127504; cranium; Loc. 1; $\times 2$. 6, NI 127505; small librigena; Loc. 1; $\times 6$. 9, NI 127506; exoskeleton; Loc. 1; $\times 0.55$.
 Fig. 7. *Microparia* (*Microparia*) cf. *prantli* Marek, 1961; Loc. 3, Member 3; NI 127510; pygidium; $\times 5$.
 Fig. 8. *Pricyclopyge obscura* Marek, 1961; Loc. 3, Member 3; NI 127511; pygidium, latex cast from external mould; $\times 2$.



the glabella (Lu 1975, pl. 9, fig. 7); all these features depend on state of preservation. Specimens from Western Yunnan exhibit similar characters and the determination can be made with some confidence.

Isoteloidea liangshanensis differs from the type species of *Liomegalaspides*, *L. usuii* (Yabe, in Yabe and Hayasaka, 1920, p. 57, pl. 18, fig. 9; pl. 19, fig. 8; Kobayashi 1951, p. 27, pl. 2, figs 7-8; Lu, in Lu and Chang 1974, p. 126, pl. 50, figs 1-2; Lu 1975, p. 328, pl. 13, figs 1-7) from the uppermost Dawan Formation (uppermost Arenig) of western Hubei, mainly in the less effaced axial furrows on the cranium. The species was referred to *Liomegalaspides* and is considered to be a junior subjective synonym of *L. blackwelderi* (Weller) by Zhou *et al.* (in press). The holotype cranium of the latter species, refigured by Chang and Jell (1983), agrees closely with that of *liangshanensis* and the sole difference, a poorly defined anterior border, may be due to the preservation of *blackwelderi* in limestone and *liangshanensis* in shale.

Subfamily OGYGIACARIDINAE Raymond, 1937

Genus OGYGINUS Raymond, 1912

Type species. Asaphus cordensis Murchison, 1839.

Ogyginus daliensis (Sheng, 1974b)

Plate 1, figures 10, 12-14; Plate 2, figures 1-6, 9

1974b *Hoekaspis daliensis* Sheng, p. 100, pl. 2, fig. 1a-e; pl. 3, fig. 1a-e.

1974b *Hoekaspis daliensis ovatus* Sheng, p. 100, pl. 1, fig. 5a-d; pl. 2, fig. 2a-e.

Lectotype. Selected herein: BGM OT68-29, figured Sheng (1974b, pl. 2, fig. 1c), an exoskeleton lacking librigenae, from Member 1 of the Hsiangyang Formation, Loc. 1.

Figured specimens. Two exoskeletons (NI 127503, 127506), two cranidia (NI 127501, 127504), one pygidium (NI 127496), one hypostoma with attached cephalic doublure (NI 127500) and one small librigena (NI 127505), from Member 1, Loc. 1; one exoskeleton without librigenae (NI 127502) from Member 1, Loc. 2; one meraspid (degree 7) exoskeleton (NI 127498), one pygidium (NI 127497) and one hypostoma (NI 127499) from Member 2, Loc. 1.

Description. Exoskeleton oval in outline, 62-72 per cent. as wide as long. Cephalon sub-semicircular, its width less than twice the length (sag.) excluding librigenal spines. Glabella gently convex, declines anteriorly towards shallow preglabellar furrow, narrows slightly until level with rear end of palpebral lobe and then expands forwards to attain maximum width 66-73 per cent. of glabellar length in most of the less compressed specimens. Lateral glabellar furrows rarely preserved, seen as faint impressions on only a few specimens (Pl. 2, fig. 3). S0 curves backwards near sagittal line to meet posterior band furrow of occipital ring. S1-S4 short (tr.), directed more or less adaxially, and do not reach axial furrow abaxially. S1 elliptical, level with point 40 per cent. of glabellar length from rear; S2-S4 triangular (S4 very narrow (exsag.)), sited, respectively, opposite front, mid-point and posterior end of palpebral lobe. Baccula elongate, weakly defined by furrow adaxially, and extends along axial furrow between S0 and S1. Occipital ring consists of pair of weakly defined, sub-triangular lateral lobes, and posterior band which narrows abaxially. Median glabellar node situated between lateral occipital lobes and immediately in front of shallow posterior band furrow. Axial furrow deep, wide; preglabellar furrow broadly curved, deep abaxially but shallower medially. Palpebral lobe reniform, well defined by distinct palpebral furrow in some specimens (Pl. 2, fig. 2), its length usually 14 per cent. that of cranium and 11 per cent. in large examples (Pl. 2, fig. 9); it is generally located opposite mid-point of cranium, but two-thirds overall length from rear in large specimens, and anterior end is close to axial furrow; ocular ridge short, thick, runs forwards and slightly adaxially (Pl. 2, fig. 2). Anterior area of fixigena narrow (tr.), adaxially declined, seen to merge frontally with anterior border in well-preserved specimens; palpebral area slightly convex; posterior area wide (exsag.), equilaterally triangular in outline, with convex border that is well demarcated by deep, wide

border furrow and narrows adaxially. Anterior border convex laterally, becoming narrower (sag.) and flatter adaxially. Anterior sections of facial suture run divergently into anterior border, where they curve adaxially to converge at 120° and meet frontally in a gentle curve; posterior sections form broadly divergent, sigmoidal curves as far as border furrow, where they turn sharply adaxially to cut posterior border. Cranial doublure ventrally convex, narrows adaxially, and carries a few parallel, fine terrace ridges.

Librigena with narrow, vertical eye socle; lateral and posterior borders convex, well defined by deep, wide border furrows, and widen towards genal angle, where they join to form a short, broadly based librigenial spine that, in smaller specimens, is relatively longer, more narrowly based, and slightly curved inwards. Hypostoma broadly rounded anteriorly, its length three-quarters the width, with acuminate but entire posterior margin. Middle body convex, wider than long, separated from large, triangular anterior wing by shallow, broad anterior border furrow but well defined by shallow lateral border furrow and deep, wide posterior border furrow; anterior lobe sub-oval, its length 80 per cent. that of hypostoma, and its posterolateral margin slightly concave abaxially; posterior lobe crescentic, short (sag.); middle furrow V-shaped, wide, mostly deep but shallows adaxially from maculae; macula prominent, located on anterior flank of posterior lobe, nearer to sagittal line than to lateral margin. Lateral border convex, wider than posterior border. Surface, except for maculae, covered with widely spaced, arched terrace ridges, subparallel to lateral and posterior margins.

Thorax with zetoidal axial furrows. Axis gently convex, 30–33 per cent. the thoracic length in large specimens, and narrows slightly from fifth ring backwards; each axial ring is trapezoidal in plan, uniformly wide (sag.). Pleura truncated distally, with deep, spindle-shaped pleural furrow which ends opposite fulcrum.

Pygidium sub-semicircular in outline, the length 51–60 per cent. the width in well-preserved specimens; in compressed examples the corresponding figure is 38–48 per cent. (Pl. 1, fig. 10). Axis convex, conical, reaches paradoublure line posteriorly, and has frontal width about one-quarter that of pygidium; articulating ring furrow distinct; six or seven axial rings and a terminal piece are visible on most material and only three rings in large specimens, but up to 11 rings are seen in some internal moulds. Axial furrows usually distinct, but more or less effaced in large specimens. Pleural region gently convex with six unfurrowed, distally rounded ribs; articulating half-rib ridge-like, well defined by deep, spindle-shaped first pleural furrow. Pygidial border flat or weakly convex, delimited by border furrow which appears deep or shallow, depending on preservation. Doublure narrow, 15–18 per cent. the pygidial length medially but widens slightly abaxially; inner margin subparallel to that of pygidium, and surface covered with closely spaced, fine terrace ridges subparallel to margin.

A meraspid exoskeleton (Pl. 1, fig. 13) is similar to the adult but differs in the larger palpebral lobe, the almost parallel-sided glabella, the presence of an intergenal angle on the librigena, and the slightly but uniformly tapered thoracic axis.

Remarks. Specimens in our large collection are mostly compressed or deformed, the better preserved material forming the basis of the above description, and it is clear that the supposedly different morphological forms (for example, *Hoekaspis daliensis ovatus* Sheng, 1974b, p. 100, which has a slightly shorter exoskeleton) found together at several stratigraphical levels belong to a single species. The lectotype selected herein for *ovatus* is a pygidium (Sheng 1974b, pl. 2, fig. 2d) identical to some in our collection (Pl. 1, fig. 10); it is 40 per cent. as long as wide, much wider than specimens preserved in relief and the result, we believe, of different preservation.

Sheng (1974b) referred *daliensis* to *Hoekaspis* Kobayashi, 1937 and noted only briefly that it is almost identical to *H. megacantha* (Leanza, 1941) (see Harrington and Leanza 1957, p. 179, figs 88–89). Differences between the two forms lie mainly in the slightly wider glabella and much fainter pygidial pleural furrows of the Argentine species. The type species of *Hoekaspis*, *Megalaspis matacensis* Hoek, in Steinmann and Hoek, 1912 from the Llanvirn of Bolivia, was re-illustrated by Ross (1965, pl. 8, figs 8–9, 12–13, 16, 19) and a neotype pygidium was designated by Příbyl and Vaněk (1980, p. 26, pl. 23, fig. 2). Fortey and Owens (1978, p. 261) considered that *H. matacensis* differed from *H. megacantha* in having a wider pygidium with unfurrowed pleural field, and an extremely narrow (sag.) anterior cranial border, and they assigned the latter species to *Merlinia*, a point of view contested by Příbyl and Vaněk (1980, p. 29). *Merlinia* as established by Fortey and Owens (1978) included several Welsh Arenig species and a Llanvirn species from England described by Rushton and Hughes (1981). It is closely allied to *Ogyginus* and, as noted by Fortey and Owens (1987, p. 142), at least one early member of the latter genus, *O. hybridus* (Salter, 1866), has characters intermediate between *Ogyginus* and *Merlinia*. The cranidium of *Hoekaspis megacantha*

differs from that of the type species of *Merlinia*, *M. rhyakos* Fortey and Owens, 1978 (p. 263, pl. 5, figs 1–6; pl. 6, figs 1–5), in having a shorter glabella, more expanded anteriorly, a narrower (sag.) anterior border, and the anterior area of the fixigena merges with the abaxial part of the anterior border, seen only on a less compressed specimen figured by Harrington and Leanza (1957, fig. 89, 1). All these characters are typical of *Ogyginus*.

In addition to the type species and *H. megacantha*, at least two other Llanvirn forms have been included in *Hoekaspis*: *H. schlagintweiti* Harrington and Leanza, 1942 (p. 135, pl. 1, figs 2–5, 7–9; 1957, p. 177, fig. 87, 1–6) from Argentina and *H. yahuari* Příbyl and Vaněk, 1980 (p. 27, pl. 13, figs 1–2; pl. 14, fig. 6) from Bolivia, Argentina and Peru. All these South American species have a cephalon similar to that of *Ogyginus*, six ribs are visible on the pleural region of the pygidium (and can even be traced on the neotype of *H. matacensis*), but are usually more weakly defined compared with those in most species of *Ogyginus*. In our opinion the effacement of pleural furrows is not a reliable generic character and some species of *Ogyginus*, such as *O. hybridus* (Salter, 1866) (see Fortey and Owens 1987, p. 143, figs 29–32) and *O. orbensis* Courtessole, Pillet, Vizcaino and Eschard, 1985 (p. 44, pl. 6, figs 1–8), show similar pleural furrows. The distinctness of pleural furrows may vary during ontogeny (Fortey and Owens 1987, p. 146) or with preservation; in *O. terranovicus* Dean, in Dean and Martin, 1978 (p. 15, pl. 5, fig. 9; pl. 6, figs 4, 6–7) from Arenig clastics at Bell Island, eastern Newfoundland, testaceous specimens exhibit much fainter pleural furrows than internal moulds. Unfortunately, the hypostoma is not known in *Hoekaspis*, but judging from the rest of the exoskeleton, we believe the genus may eventually prove synonymous with *Ogyginus*.

Hoekaspis daliensis possesses features diagnostic of *Ogyginus* as defined by Whittard (1964, p. 245) and by Fortey and Owens (1987, p. 142), and is transferred to the latter genus. *Ogyginus cordensis* (Murchison), from the Llanvirn–lower Llandeilo of west Shropshire and central Wales, was redescribed by Whittard (1964, p. 250, pl. 42, figs 2–8; pl. 43, figs 2–11) and by Hughes (1979, p. 126, figs 21–61, 66), who included Whittard's varieties *septenarius* and *novenarius* in the synonymy. *O. daliensis* resembles the Anglo-Welsh species in many respects but differs in the more anteriorly sited palpebral lobe, the longer (exsag.) posterior area of the fixigena, and the wider thoracic axis (in large specimens about one-third the width of the thorax, compared with one-quarter). In addition, the pygidium of *O. cordensis* possesses eight or nine pleural ribs, compared with six or seven in *O. daliensis*, and has a narrower axis.

Among the other species of *Ogyginus* listed by Fortey and Owens (1987, p. 142) and by Rabano (1990, p. 70) is the closely related *O. armoricanus* (de Tromelin and Lebesconte, 1876) (see Henry 1971, p. 66, pl. 1, figs 1–11, text-figs 1–2; 1980, p. 37, fig. 7, pl. 1, figs 4–5, 7) from the Arenig to, possibly, lower Llanvirn of Brittany, France. The French species is distinguished only by the slightly greater glabellar width (76 per cent. of length, compared with 66–73 per cent.), the narrower (sag.) anterior border, the smaller anterior wing of the hypostoma and, probably, the slightly larger palpebral lobe, all apparent differences that may be due to preservation. Only a few specimens of *O. armoricanus* have been described, the intraspecific variation is not known, and for the time being we retain *O. daliensis* as a separate taxon.

EXPLANATION OF PLATE 3

Fig. 1. *Cyclopyge* sp.; Loc. 3, Member 3; NI 127509; exoskeleton; $\times 4$.

Figs 2, 5. *Hungioides* cf. *bohemicus* (Novák, in Perner, 1918); Member 1. 2, NI 127507; pygidium; Loc. 2; $\times 3$. 5, NI 127508; incomplete cranidium; Loc. 1; $\times 1$.

Figs 3–4, 6–8, 10–11. *Hanchungolithus xiangyangensis* Sheng, 1974b; Loc. 1, Member 2. 3, NI 127513; exoskeleton; $\times 6$. 4, NI 127514; exoskeleton; $\times 6$. 6, NI 127515; cephalon; $\times 5$. 7, NI 127516; lower lamella of fringe; $\times 6$. 8, NI 127517; cephalon; $\times 8$. 10, NI 127518; cephalon with two attached thoracic segments; $\times 5$. 11, NI 127519; exoskeleton; $\times 6$.

Fig. 9. *Pricyclopyge obscura* Marek, 1961; Loc. 3, Member 3; NI 127512; cranidium; $\times 3$.



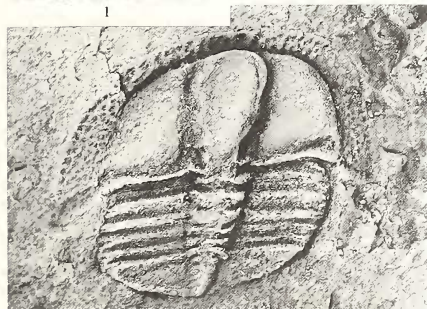
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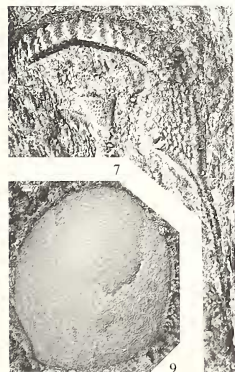
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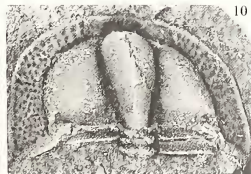
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11

Family DIKELOEPHALINIDAE Kobayashi, 1936

Genus HUNGIOIDES Kobayashi, 1936

(= *Argentinops* Přibyl and Vaněk, 1980)*Type species. Dicellocéphalina bohémica* Novák, in Perner, 1918.*Hungioides cf. bohemicus* (Novák, in Perner, 1918)

Plate 3, figures 2, 5

1974b *Taihungshania* sp., Sheng, p. 102, pl. 4, fig. 5*Figured specimens.* One incomplete cranidium (NI 127508) from Member 1, Loc. 1; one pygidium (NI 127507) from Member 1, Loc. 2.

Description and remarks. Specimens are fragmentary and more or less compressed. The glabella narrows gently forwards, bluntly rounded frontally, with four pairs of lateral glabellar furrows which, except for S4, become fainter before reaching the axial furrow; S1 is bifurcate adaxially, S4 is shortest, sited opposite adaxial end of the eye ridge. S0 is deep and transverse, defining a uniformly wide (sag.) occipital ring. A prominent pair of depressed, oval alae has the anterior ends opposite the distal end of S2. Surface of the cranidium covered with dense granulation that becomes finer on the fixigena. The large pygidium described by Sheng (1974b) as *Taihungshania* sp., from the same bed at Locality 1 as the present figured cranidium, is about 50 mm long, wider than long, with nine or ten pleural ribs in addition to the articulating half-rib. The axis has at least 11 well-defined rings, and the outer pair of marginal spines extends backwards with its tips about level with that of the axis. The smaller figured pygidium, 18 mm long, closely resembles the larger specimen but the two pairs of broad based marginal spines end in-line. We agree with Rabano (1983, p. 436) that such a difference is due to ontogenetic variation during the holaspis stage.

The cranidium has a more uniformly parabolic glabellar outline than *Hungioides mirus* Lu, 1975 (p. 372, pl. 29, figs 8–15) from the upper Arenig of Hubei and Guizhou, China, and *H. acutinasus* Fortey and Shergold, 1984 (p. 345, pl. 44, figs 1–7) from the Nora Formation (Arenig) of central Australia, but is generally comparable to that of *H. bohemicus* (Novák, in Perner 1918, pl. 1, fig. 6; see also Rabano 1983, pl. 1, figs 1–3; 1990, pl. 11, figs 1–3). The pygidium closely resembles the Bohemian lectotype (Perner 1918, pl. 1, fig. 4; selected by Marek, in Horný and Bastl 1970, p. 77, pl. 5, fig. 7), and specimens from the Llanvirn of Spain figured by Rabano (1983, pl. 1, figs 4–6; 1990, pl. 11, figs 4–7), especially in the pleural field, with nine or ten segments, and in the form of the marginal spines. Rabano (1983, p. 435) reassigned to *H. bohemicus* several other Llanvirn, or possibly Llanvirn, forms, including: *H. bohemicus arouquensis* Thadeu, 1956 (p. 11, pl. 2, figs 1–2; pl. 6, fig. 3) from Portugal, and *H. novaki* Kobayashi, 1936 (based on Perner 1918, pl. 1, fig. 5; see Prantl and Přibyl 1948, p. 15, pl. 2, fig. 1) from Bohemia, and considered their supposedly different characters to be the result of ontogenetic changes. *Hungioides graphicus* R. and E. Richter, 1954a (p. 341, pl. 1, figs 1–4) from the Griffelschiefer (upper Arenig–Llanvirn, according to Sdzuy 1971) of Thuringia, is based on poorly preserved pygidia and thoracic segments but, as noted by Fortey and Shergold (1984, p. 348), it is closely comparable to the type species.

Hungioides intermedius (Harrington and Leanza, 1957, p. 191, fig. 100, 1–8), from the Llanvirn of Argentina, was made type species of *Argentinops* Přibyl and Vaněk, 1980, considered to be a junior subjective synonym of *Hungioides* (Rabano 1983; Fortey and Shergold 1984). It differs from the present form mainly in the more slender outer pair of spines, located at the posterolateral corners of the pygidium.

From the above discussion the Chinese form is best compared with the *Hungioides bohemicus* species-group. Authorship of the species has been variously attributed by Prantl and Přibyl (1948,

p. 14), Lochman-Balk in Moore (1959, p. O361) and Rabano (1983, p. 436; 1990, p. 83); in the present paper we follow Rabano (1990).

Family CYCLOPYGIDAE Raymond, 1925

Genus CYCLOPYGE Hawle and Corda, 1847

Type species. Egle rediviva Barrande, 1846.

Cyclopyge sp.

Plate 3, figure 1

Figured specimen. Exoskeleton (NI 127509) from Member 3, Loc. 3.

Remarks. The material is poorly preserved but the presence of a prominent S1 and a pair of circular swellings behind it suggests assignment to *Cyclopyge*. The figured specimen has four thoracic segments preserved and the cranium is slightly displaced, indicating a moulted exoskeleton. The pygidium is longer and more narrowly rounded posteriorly compared with most species of *Cyclopyge*, but is similar to that of *C. kossleri* (Klouček, 1916) from the Llanvirn of Bohemia and South Wales (Marek 1961, p. 25, pl. 1, figs 14–17; Fortey and Owens 1987, p. 155, fig. 37a–b). Three pairs of pleural furrows are visible on the same specimen, a character typical of *C. kossleri*, but the axis of the European species is longer, almost pointed posteriorly, and has probably one more ring.

Genus PRICYCLOPYGE R. and E. Richter, 1954b

(= *Pricyclopyge* (*Bicyclopyge*) Hörbinger and Vaněk, 1985)

Type species. Aeglina prisca Barrande, 1872.

Remarks. We follow Fortey and Owens (1987, p. 181) in considering the subgenus *Bicyclopyge* to be a junior subjective synonym of *Pricyclopyge sensu stricto*.

Pricyclopyge obscura Marek, 1961

Plate 2, figure 8; Plate 3, figure 9

1961 *Pricyclopyge obscura* Marek, p. 35, pl. 2, fig. 17; text-fig. 10.

Holotype. Cranium (SBNM BR132), figured Marek (1961, pl. 2, fig. 17), from the Šárka Formation (Llanvirn) at Šárka, Prague.

Figured specimens. One cranium (NI 127512) and one pygidium (NI 127511) from Member 3, Loc. 3.

Description and remarks. Only two examples were previously known of the cranium, which was fully described by Marek and differs from that of other species of *Pricyclopyge* in having an oval outline, only gently tapered to both front and rear. The present specimen agrees closely with the holotype; the median node is slightly elongate, sited in the centre of the glabella; a pair of indistinct swellings is visible near the posterior margin; and three pairs of very faint, eyebrow-shaped impressions can be traced on the posterior flanks.

The pygidium in our collection is triangular in outline, about twice as wide as long, narrowly rounded posteriorly with slightly concave lateral margins. The axis occupies 25 per cent. the anterior width and 64 per cent. the length of the pygidium, and is gently tapered, with a well-defined, rim-like articulating half-ring and broadly-rounded tip; a single, transversely straight ring furrow is

complete, followed by a second ring furrow that is defined only distally. The pleural field is gently declined abaxially, and the articulating half-rib is straight and ridge-like. The border is convex, uniformly wide, one-tenth of the pygidial length (sag.), well defined by a deep border furrow.

Apart from its slightly shorter axis, the pygidium is almost indistinguishable from that of *Pricyclopyge binodosa prisca* (Barrande, 1872) (Marek 1961, pl. 1, fig. 20, as *P. binodosa binodosa*; Hörbinger and Vaněk 1985, pl. 2, figs 1–3, as *P. prisca prisca*; for discussion of subspecies name see: Marek 1961, p. 33; Whittard 1966, p. 287; Rushton and Hughes 1981, p. 633; and Fortey and Owens 1987, p. 181). The present pygidium also agrees closely with Chinese material described as *P. prisca* and *P. sichuanensis* by Lee (1978, p. 252, pl. 107, fig. 9 and figs 7–8 respectively) from the Llanvirn of Moli, western Sichuan, specimens of which are slightly deformed but show a pair of thoracic spines on the sixth segment. In the absence of the cranidium it is impossible to decide whether both should be assigned to *P. binodosa prisca* or to *P. obscura*.

Genus MICROPARIA Hawle and Corda, 1847

Type species. Microparia speciosa Hawle and Corda, 1847.

Subgenus MICROPARIA (MICROPARIA) Hawle and Corda, 1847

Microparia (Microparia) cf. prantli Marek, 1961

Plate 2, figure 7

Figured specimen. One pygidium (NI 127510) from Member 3, Loc. 3.

Description. Pygidium sub-semicircular in outline, 76 per cent. as long as wide, moderately convex. Axis occupies 44 per cent. of pygidial width frontally and is strongly tapered; two axial rings are delimited by shallow ring furrows; distinct, rim-like articulating half-ring is defined by deep, wide (sag.) articulating furrow. Axial furrows clearly defined anteriorly and become faint behind the third axial ring. Pleural region almost featureless except for ridge-like articulating half-rib, defined by prominent anterior pleural furrow. Border narrow, visible only laterally, delimited by shallow, broad border furrow. Doublure uniformly wide (sag.), wider than border and equal to about 16 per cent. of pygidial length (sag.).

Remarks. Cranidia in our collection are badly deformed. Pygidial features suggest that the form is referable to *Microparia*, a genus divided by Fortey and Owens (1987) into two subgenera, *Microparia sensu stricto* and *M. (Heterocyclopyge)* Marek, 1961. Zhou *et al.* (1994) considered *Quadratapyge* Zhou, in Zhou *et al.*, 1977 to be a third subgenus of *Microparia*. Species of *Heterocyclopyge* and *Quadratapyge* have a pygidium that is straight-sided laterally, with an entire axis, and are quite different from the present form. In the outline, length/width ratio, and form of the axis, particularly in specimens of comparable size, the pygidium closely resembles that of *M. (M.) broeggeri* (Holub, 1912) (see Marek 1961, p. 45, pl. 3, fig. 16; Fortey and Owens 1987, p. 164, figs 44a–e, 45a–e) from the Klabava Formation of Bohemia and the upper Arenig (Fennian Stage) of South Wales, and of *M. (M.) prantli* Marek, 1961 (p. 40, pl. 3, figs 1–4, text-fig. 13) from the Šárka Formation (Llanvirn) of Bohemia. However, the doublure of *M. (M.) broeggeri* widens adaxially (Fortey and Owens 1987, p. 166) compared with its uniform width in *M. (M.) prantli*, and we consider our form to be closer to the latter species.

Family TRINUCLEIDAE Hawle and Corda, 1847

Subfamily HANCHUNGOLITHINAE Lu, 1963

Genus HANCHUNGOLITHUS Lu, 1954

Type species. Crytolithus multiseriatus Endo, 1932.

Hanchungolithus xiangyangensis Sheng, 1974b

Plate 3, figure 3-4, 6-8, 10-11

1974b *Hanchungolithus xiangyangensis* Sheng, p. 106, pl. 6, fig. 4a-i.1989 *Hanchungolithus xiangyangensis* Sheng; Zhou and Hughes, p. 61.

Lectotype. Selected by Zhou and Hughes (1989, p. 61). Exoskeleton BGM OT68-90, figured Sheng (1974b, pl. 6, fig. 4b), from Member 2 of the Hsiangyang Formation, Loc. 1.

Figured specimens. Three exoskeletons (NI 127513-127514, 127519), two cephalae (NI 127515, 127517), one cephalon with two attached thoracic segments (NI 157518), and one lower fringe lamella (NI 157516); all from Member 2, Loc. 1.

Description. Exoskeleton oval in outline. Cephalon sub-semicircular, 40-53 per cent. as long as wide (excluding librigenal spines) in well preserved specimens. Glabella clavate, strongly convex, protruding slightly into the fringe anteriorly, with median node on apex at mid-length; S1-S3 oval to circular, sited abaxially, becoming successively shallower; S3 in-line with median node. Occipital ring narrow (sag.), uniformly wide, arched posteriorly and well defined by deep S0. Axial furrow deep, wide. Small, low baccula is elongate, oval, with anterior end close to S2. Cheek convex, declined both abaxially and adaxially; lateral eye tubercle distinct, located close to axial furrow and behind line through S3 and median node; eye ridge runs slightly forwards adaxially to axial furrow; slender genal ridge extends diagonally to posterolateral corner of cheek; posterior border narrow (exsag.), upturned; posterior border furrow broad, deep, ends in posterior fossula.

Fringe flat, narrow (sag.) anteriorly but widens gradually to posterior margin, where its breadth is twice that in front of glabella; marginal band distinct. Lower lamella is prolonged backwards at genal angle to form librigenal spine which is slightly curved inwards, its tip well beyond the posterior margin of the pygidium. Fringe pits largest frontally and become slightly smaller both inwards and laterally; they are radially arranged in weak sulci, from about R9 to R11, and become irregularly arranged abaxially; there are about four arcs in front of the glabella, and seven to ten pits along the posterior margin. I_1 and I_n are complete; in specimens where the pits are clearly visible, I_1 has 24-28 pits and I_n 22-24; pits between I_1 and I_n are mostly irregular, but a roughly regular arrangement is seen in I_2 1-16 and I_3 1-12.

Thoracic axis well defined, strongly convex transversely, gradually tapered backwards and about 25 per cent. of thoracic width; each ring is uniformly wide (sag.) with pair of deeply incised apodemal pits at its anterolateral corners. Pleural region flat, narrows slightly backwards; each pleura parallel-sided, horizontal for most of its length as far as fulcrum, where it turns downwards; pleural furrow wide, shallow, and almost straight.

Pygidium sub-triangular, 25-31 per cent. as long as wide. Axis convex, conical, occupying 19-22 per cent. of frontal width of pygidium and reaching inner margin of border; there are five axial rings and a terminal piece, and the ring furrows become successively weaker posteriorly. Pleural region flat, with only one pleural furrow, which is shallow, widens abaxially and delimits clearly an upturned articulating half-rib. Border ridge-like in plan view, narrows abaxially, and is deflected ventrally.

Remarks. More than seven Chinese species of *Hanchungolithus* were reviewed by Zhou and Hughes (1989), six of them of late Arenig age from the Yangtze region. *H. xiangyangensis* is the youngest of the seven, and its most distinctive character is the more regular arrangement of pits on the anterior and anterolateral parts of the fringe (Zhou and Hughes 1989, pp. 58, 74). Previous descriptions were incomplete, and the above account is based mainly on new material in our collection.

Family CALYMENIDAE Milne Edwards, 1840

Subfamily REEDOCALYMENINAE Hupé, 1955

Genus NESEURETUS Hicks, 1873

Type species. *Neseuretus ramseyensis* Hicks, 1873.

Remarks. More than 50 species have been referred to this genus, most of which were listed by Fortey and Morris (1982) and Rabano (1990). Only a few have been revised (Whittard 1960; Fortey

and Owens 1987; Rabano 1990), and both *N. antetrastani* Dean, 1966 and *N. lugneensis* Courtessole, Pillet and Vizcaino, 1983 were reassigned to *Pradoella* Hammann, 1977 by Hammann (1983), Rabano (1990) and Courtessole *et al.* (1991).

Nineteen species and subspecies of *Neseuretus* have been described from Southwest and Central China, and the species *yinganensis*, listed as a *nomen nudum* by Fortey and Morris (1982), had in fact been published as *Calymenesun yinganensis* Zhang, 1981 (p. 211, pl. 78, figs 3–5). Most of the Chinese species are known from only a few specimens. The present collection indicates that the presence or absence of S4 and hypostomal pits, and the form of the preglabellar area and anterior border furrow may vary within a single species and, as noted by Whittington (1966) and Fortey and Owens (1987), apparent intraspecific variation is largely dependent on preservation. In the following descriptions, most of the Chinese species are reviewed.

Neseuretus birmanicus (Reed, 1906, p. 71, pl. 6, fig. 27), from the Naungkangyi Beds of the northern Shan States, Burma, was founded on a compressed cranidium. Lu *et al.* (1965, p. 619, pl. 128, fig. 13) and Sheng (1974b, p. 112, pl. 8, fig. 2a–b, d, f, non 2c, e, g) redescribed the species using several specimens from the Llanvirn of Baoshan, western Yunnan, an area that belongs to the same structural unit (now called the Sibumasu Terrane) as the northern Shan States. The Chinese specimens indicate that, as noted by Fortey and Morris (1982), *N. birmanicus* Reed, 1906 closely resembles *N. tristani* (Brongniart, in Desmarest, 1817), redescribed in detail by Henry (1970, 1980), Sadler (1974), Hammann (1983) and Rabano (1990), but differs in the more developed anterior border furrow. This may be due to preservation, and better preserved topotype material is needed for further comparison.

Burmese and Afghanistan specimens later referred to *birmanicus* by Reed (1915, p. 44, pl. 8, figs 1–5, as *Calymene birmanica*) and by Pillet and de Lapparent (1969, p. 325, pl. 34, figs 1–10; ?pl. 35, fig. 9, as *Diacalymene birmanicus*) are quite different from the holotype. As noted by Dean (1967a, p. 117; 1975, p. 369) they resemble *Neseuretus (Neseuretinus) turcicus* Dean (1967a, p. 115, ?pl. 7, figs 8, 10–11; pl. 9, figs 1–4), from the Caradoc of south-eastern Turkey, but differ from the latter in the shorter, broadly rounded (rather than pointed) anterior border and the less convex preglabellar field. These characters, in turn, match *Vietnamia douvillei* (Mansuy) (see Kobayashi 1960, p. 44, pl. 5, figs 4–5) and we reassign *birmanicus sensu* Reed, 1915 questionably to *Vietnamia*. *Calymene nivalis* Salter, in Salter and Blandford, 1865 from the 'middle Ordovician' of the central Himalayas, India, was referred to *Neseuretus* by Dean (1967b, p. 32; 1975, p. 368) and by Morris and Fortey (1985, p. 96, pl. 5, fig. 3), but may possibly be referable to *Neseuretinus*, as may *Pharostoma malestana* Wolfart (1970, p. 82, pl. 17, figs 2–7) from the middle Ordovician of east Afghanistan (Dean 1975, p. 369). *Neseuretinus* is possibly present in South Tianshan, formerly part of the USSR (as *Calymenesun* and *Synhomalonotus*; see Kolobova 1978, pp. 133, 134, pl. 26, figs 1–5 and 6–11 respectively; see also Zhou and Dean 1989, p. 133). *Synhomalonotus pamiricus* Balashova (1966, p. 233, pl. 2, figs 12–15) from the middle Ordovician of Pamir has a glabella with swollen, wide L1 and may be related to *Neseuretinus* or *Vietnamia*, but the figured specimens do not show the rest of the cranidium and identification is uncertain.

Neseuretus cf. tungtzuensis (Sheng, 1958)

Plate 4, figures 5, 7, 10

Figured specimens. One cranidium (NI 127528) from Member 1, Loc. 1; one cranidium (NI 127527), one librigena (NI 127526) and one pygidium (NI 127529) from Member 1, Loc. 2.

Remarks. Specimens from lower levels in Member 1 of the Hsiangyang Formation are recorded here for the first time. The cranidium is almost identical with the lectotype (selected herein, BGM Loc. Sh. 173, figured Sheng 1958, pl. 7, fig. 5a) of *Calymene (Synhomalonotus) tungtzuensis*, but has a slightly more tapered glabella. The pygidium has six well-defined axial rings and six ribs; it closely resembles that in the original material (Sheng 1958, p. 200, pl. 7, fig. 5a–c), but according to Sheng's original description the latter has at least eight distinct axial rings. The form of the glabella and

librigena recalls *N. shensiensis* (Lu, 1957, p. 288, pl. 150, figs 13–16; 1975, p. 452, pl. 46, fig. 3; pl. 47, figs 6–11; pl. 50, fig. 11) from the Chaochiapa Formation (middle Arenig) of southern Shaanxi, but *shensiensis* has a smaller palpebral lobe, located opposite L3, and a correspondingly longer (exsag.) fixigena. The pygidium of *shensiensis* exhibits only four or five ribs on the inner part of the pleural region, adaxial to the fulcrum. On the basis of the glabella and preglabellar area, *N. kayseri* (Kobayashi, 1951, p. 41, pl. 3, fig. 7), from northern Sichuan, may be closely related to *N. shensiensis*, but the single cranidium is incomplete and difficult to interpret. *Neseuretus caerhunensis* Beckly, 1989 (p. 15, figs 14a–1, 15a–d), from the upper Arenig of North Wales, is generally similar to the present form but differs in the much longer preglabellar area, wider palpebral area, and the oblique rather than transverse eye ridge. A large, well-preserved pygidium shows that the Welsh species has up to nine axial rings.

N. tungtzuensis, from the upper Arenig of northern Guizhou, is similar to a number of contemporaneous forms such as *N. concavus* Lu, 1975 (p. 454, pl. 47, figs 13–15; pl. 48, fig. 1), *N. cf. shensiensis* (Lu, 1975, p. 454, pl. 47, fig. 12), *N. concavus tenellus* Lu, 1975 (p. 242, pl. 48, figs 2–6), *N. expansus* Lu, 1975 (p. 456, pl. 48, figs 8–10) and *N. equalis* Lu, in Lu and Chang, 1974 (p. 130, pl. 51, figs 13–14), all from southern Shaanxi except for *N. equalis*, which is from north-eastern Sichuan. The cranidium in these species is of *ramseyensis* or *murchisoni* type, including: shorter (sag.), straight-sided, truncated glabella; longer preglabellar area; larger palpebral lobe, sited more posteriorly (opposite L3 and front part of L2); and shorter (exsag.) posterior area of fixigena. Judging from illustrations of *N. concavus*, *N. concavus tenellus* and *N. expansus*, the pygidium has about eight axial rings and six pleural ribs; according to Fortey and Owens (1987) the corresponding numbers are eight to ten and seven to nine for *N. ramseyensis*, and five and four for *N. murchisoni* (Salter, 1865). We believe that forms in the *tungtzuensis* group may represent one species, and apparent differences include: the convexity of the preglabellar area and the depth of the anterior border furrow; and the presence or absence of S4 (see Lu 1975, p. 452). All of these may be the result of preservation and are probably of little specific importance, but further material of all the listed species is required.

Neseuretus elegans Lee, 1978

Plate 4, figures 1–4, 6, 12, 15

1974b *Neseuretus birmanicus* (Reed); Sheng, p. 112, pl. 8, fig. 2c only [non 2c, g = *N. elongatus* sp. nov.; non 2a–b, d, f = *N. birmanicus sensu stricto*].

1974b *Neseuretus tungtzuensis* Sheng; Sheng, p. 113, pl. 8, fig. 1a, d–e [non 1b–c = *Neseuretus elongatus* sp. nov.].

1978 *Neseuretus elegans* Lee, p. 274, pl. 107, figs 3–5.

1978 *Neseuretus leiboensis* Lee, p. 274, pl. 107, fig. 10.

Holotype. Cranidium (CIGM St196), figured Lee (1978, pl. 107, fig. 3), from the Lower Qiaojia Formation (upper Arenig–lower Llanvirn), Yanjin, north-eastern Yunnan, China.

Figured specimens. One cranidium (NI 127520) from Member 1, Loc. 2; one pygidium (NI 127523) from Member 2, Loc. 2; two cranidia (NI 127521–127522); one exoskeleton (NI 127524) and one librigena (NI 127525) from Member 2, Loc. 1.

Description and remarks. The species is closely allied to *Neseuretus arenosus* Dean, 1966 (p. 313, pl. 14, figs 1, 4–5, 7–9, 11) from the middle Arenig of the Montagne Noire, south-western France. Both have an almost identical pygidium, the pleural regions of which show five distinct ribs and a trace of a sixth, but the axis has seven well-defined rings in *N. elegans* and six in *N. arenosus*. The glabella of both species has the sides broadly curved and slightly convergent forwards, where the anterior margin is gently concave; the palpebral lobe is sited opposite L3 and part of L2, and the palpebral ridge is straight and transverse. *N. elegans* has apparently deeper axial, pre-glabellar and glabellar furrows, and S4 is present, but these differences may be due to preservation. The preglabellar area

of *N. arenosus* occupies 24 per cent. of the cranial length (sag.), compared with 30 per cent. in *N. elegans*, whilst the anterior border of the French species is slightly shorter, and for these reasons we retain the two specific names. Additional specimens from the Montagne Noire were subsequently referred to *N. arenosus* (Courtessole *et al.* 1983, p. 25, pl. 1, figs 1–9; pl. 6, figs 1–8, 11–12; see also pl. 2, fig. 15, as *Platycalymene* (*Platycalymene*) sp. cf. *minervensis* n. sp.; Courtessole *et al.* 1985, p. 47, pl. 8, figs 3–4; see also pl. 8, fig. 11, as *Platycalymene* (*Platycalymene*) sp. cf. *minervensis* n. sp.). Most were later considered to be distinct from the holotype and redetermined as *N. cf. arenosus* by Courtessole *et al.* (1991). Well-preserved specimens assigned to *N. cf. arenosus* by Courtessole *et al.* (1991, p. 9, pl. 4, figs 5–8, text-fig. 4) agree closely with those of *N. elegans*, including the length of the preglabellar area. Courtessole *et al.* (1991, p. 10) claimed that *N. cf. arenosus* differs from *N. arenosus sensu stricto* in having a better developed preglabellar furrow, longer preglabellar area, and a shorter palpebral lobe sited further forwards, with posterior end opposite S2. However, our collection shows that at least the palpebral lobe varies in both size and position during ontogeny; it is larger and more posteriorly sited in small holaspids (Pl. 4, fig. 4) and late meraspids (Pl. 4, fig. 12, meraspid degree 12). If it can eventually be demonstrated that the supposedly distinctive characters of the French species are due to intraspecific variation, ontogenetic variation and preservation, we would consider *N. elegans* to be a junior subjective synonym of *N. arenosus*.

Neseuretus attenuatus Gigout, 1951 (p. 289, pl. 3, figs 6–7; see also Dean 1966, p. 317, pl. 14, figs 2, 6, 12) from, probably, the Llanvirn of Morocco resembles *N. elegans* in many respects, but is distinguished by the longer (sag.) but narrower (tr.) preglabellar area and the more convergent anterior portions of the axial furrows. No pygidium was described for the Moroccan species, but on cranial characters alone *N. attenuatus* is closer to *N. tristani* (neotype designated by Henry 1970, p. 6, pl. A, fig. 6) than to *N. arenosus* and *N. elegans*.

Neseuretus leiboensis Lee from the Lower Qiaojia Formation of western Sichuan was based on a single cranium. Lee (1978, p. 275) noted that the species has the anterior border slightly concave, apparently arched backwards rather than forwards, but is otherwise indistinguishable from *N. elegans*. Some compressed cranidia in our collection show similar deformation of the anterior border and we consider the two species to be synonymous, with *N. elegans* having line priority over *N. leiboensis*.

Neseuretus elongatus sp. nov.

Plate 4, figures 8–9, 11, 13–14, 16

- 1974b *Pseudasaphus daliensis* Sheng, pl. 4, fig. 1c–e only.
 1974b *Neseuretus birmanicus* (Reed); Sheng, p. 112, pl. 8, fig. 2e, g only.
 1974b *Neseuretus tungtzuensis* Sheng; Sheng, p. 113, pl. 8, fig. 1b–c only.

Derivation of name. From the Latin, *elongatus* (= elongate) referring to the glabellar outline.

Holotype. Cranium (NI 127532) (Pl. 4, fig. 13) from Member 2 of the Hsiangyang Formation, Loc. 1.

EXPLANATION OF PLATE 4

- Figs 1–4, 6, 12, 15. *Neseuretus elegans* Lee, 1978. 1, NI 127520; cranium; Loc. 2, Member 1; $\times 2.5$. 2–3, NI 127521; cranium, lateral and dorsal views; Loc. 1, Member 2; $\times 2$. 4, NI 127522; cranium; Loc. 1, Member 2; $\times 4$. 6, NI 127523; pygidium; Loc. 2, Member 2; $\times 2$. 12, NI 127524; small exoskeleton; Loc. 1, Member 2; $\times 4$. 15, NI 127525; librigena; Loc. 1, Member 2; $\times 4$.
- Figs 5, 7, 10. *Neseuretus cf. tungtzuensis* Sheng, 1958; Member 1. 5, NI 127526; librigena; and NI 127527; cranium; Loc. 2; $\times 2.5$. 7, NI 127528; cranium; Loc. 1; $\times 2.5$. 10, NI 127529; pygidium; Loc. 2; $\times 2.5$.
- Figs 8–9, 11, 13–14, 16. *Neseuretus elongatus* sp. nov.; Member 2. 8, 11, NI 127530; pygidium, paratype, dorsal and rear views; Loc. 1; $\times 3$. 9, NI 127531, paratype cranium; Loc. 3; $\times 6$. 13, NI 127532, holotype cranium; Loc. 1; $\times 4$. 14, NI 127533 paratype librigena; Loc. 1; $\times 5$. 16, NI 127534, paratype cranium; Loc. 1; $\times 4$.



1



2



3



4



5



6



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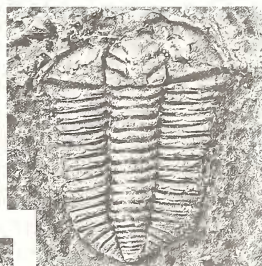
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Paratypes. One cranium (NI 127534), one librigena (NI 127533) and one pygidium (NI 127530) from Member 2, Loc. 1; one cranium (NI 127531) from Member 2, Loc. 3.

Diagnosis. *Neseuretus* species with elongate glabella and narrow (tr.) frontal area of cranium; palpebral lobe with posterior end opposite rear part of L2. Pygidial axis relatively narrow, with seven axial rings; pleural region has five furrowed ribs.

Description. Frontal area has width 34–38 per cent. that of rear of cranium. Glabella strongly convex transversely, tapers gently forwards to sharply rounded anterolateral angles and more-or-less truncate anterior margin; it occupies 25–30 per cent. the basal breadth of the cranium, about 75 per cent. the overall length, and the width of the frontal glabellar lobe is 60–65 per cent. that across L1. Occipital ring well defined by deep, wide S0 and carries median node. S1 and S2 deep; S1 curves back and becomes very shallow before reaching S0; S2 runs slightly backwards adaxially from the deep, broad axial furrow; S3 and S4 just visible on the flank of the glabella. Palpebral lobe has length 22 per cent. that of cranium and extends from opposite S3 to opposite rear of L2; palpebral ridge transverse. Anterior and palpebral areas of fixigena narrow, about 10 per cent. the posterior cranial width, and strongly declined adaxially; posterior area wide, 36–40 per cent. of maximum cranial width, sub-triangular in outline with low, weakly convex, semicircular paraglabellar area beside axial furrow and opposite L1. Anterior sections of facial suture subparallel, only slightly convergent forwards; posterior sections run abaxially in broad curve to cut posterior border at genal angle. Preglabellar field moderately swollen, merges with upturned anterior border, and defined abaxially by broad (tr.) abaxially curved furrows; anterior border furrow absent or broad (sag.) and shallow, depending on preservation. Hypostomal pits faint, sited at junction of axial and preglabellar furrows. Librigena has broad, convex lateral border, shallow border furrow, and gently declined librigenal field; eye socle crescentic, narrow, strongly upturned.

Pygidium about three-quarters as wide as long. Axis strongly convex with frontal width less than one-third that of pygidium; it includes the articulating half-ring, seven rings defined by deep ring furrows, and the terminal piece. Axial furrows deep, wide, convergent to seventh ring furrow, beyond which they are parallel, producing a funnel-shaped outline. Pleural region divided by six pleural furrows into a ridge-like articulating half-rib, five ribs and a trace of a sixth rib, and the distal half is turned down almost vertically; ribs become successively more strongly curved backwards, the fifth being subparallel to the axial furrow; interpleural furrows shallow proximally but deep on distal half of pleural region, where a narrow, unfurrowed marginal band is developed. Rear half of the margin (Pl. 4, fig. 11) marked by low rim which thickens towards sagittal line, where it merges with sub-rectangular terminal piece.

Remarks. Specimens from the same horizon and locality as *N. elongatus* were described by Sheng (1974b) as either *N. tungtzuensis* or *N. birmanicus* and are identical to the new species. One of them (Sheng, 1974b, pl. 8, fig. 2e) shows a complete thorax with attached pygidium; the thorax of 13 segments is consistent with that in other *Neseuretus* species, but the axis is narrower, occupying only one-third, or less, of the thoracic width. Of the many described species of *Neseuretus*, only a group of Chinese late Arenig forms is closely comparable to *N. elongatus*. It includes: *N. intermedius* Lu, 1975 (p. 455, pl. 48, fig. 7) and *N. sankwaichangensis* Lu, 1975 (p. 457, pl. 48, figs 11–13), both from the upper part of the Meitan Formation, southern Sichuan; *N. planus* Lu, 1975 (p. 458, pl. 46, fig. 15) from the upper part of the Meitan Formation, southern Sichuan, and the *Ningjianolithus welleri* Zone of the Siliangssu Formation, southern Shaanxi; *N. zunyiensis* Yin, in Yin and Lee, 1978 (p. 585, pl. 187, figs 4–5) from the upper part of the Meitan Formation, northern Guizhou; *N. muliensis* Lee, 1978 (p. 275, pl. 107, figs 12–13) from Muli, western Sichuan; *N. xiadongensis* Xiang and Zhou, 1987 (p. 332, pl. 39, figs 12–13) from Yichang, western Hubei; and possibly *N. conicus* (Kobayashi, 1951) (see Chang and Jell 1983, p. 207, fig. 6G), from north-western Sichuan, and *N. convexia* (sic) (Sheng, 1958, p. 201, pl. 7, fig. 6), from northern Guizhou. In all these species, as in *N. elongatus*, the glabella and anterior part of the cranium are relatively narrow, the anterior and palpebral areas of the fixigena are narrow, adaxially declined, and the posterior area is wide. The pygidium illustrated for *N. xiadongensis* matches that of *N. elongatus* but appears relatively longer due to slight compression.

The species listed above are distinguished, apparently, by their relatively shorter, more tapered glabella, and the more anterior position of the smaller palpebral lobe, opposite L3 and the front of

L2. All eight are based on inadequate or poorly preserved material and supposed differences between them may reflect their state of preservation. They may form a natural group, and some could eventually prove to be synonyms.

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